CHROMOSOMES OF THE CYCADALES

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With plates 107 and 108

THE CYCADS are the most primitive of the living gymnosperms and represent the surviving remnants of a line reaching back through the Mesozoic into the Paleozoic era. Nine genera, containing less than one hundred species, are recognized. Four of the genera occur exclusively in the western hemisphere and the other five in the eastern.

Of the western genera, *Zamia*, with twenty-six species, ranges from southern Florida to Chile. *Microcycas* is a monotypic genus and is found only in western Cuba. *Dioon*, with three species is found only in southern Mexico, and *Ceratozamia* with two species has about the same range as *Dioon*.

Of the eastern genera, *Cycas*, with eight species, ranges from Japan to Australia. *Macrozamia*, with nine species and the monotypic *Bowenia* occur in Australia. *Encephalartos*, with fourteen species and *Stangeria*, a monotypic genus, are found in southeastern Africa.

The basic chromosome number has been reported as 12 in most gymnosperms including the cycads, but recent work has shown that many of the earlier counts were incorrect (Sax and Sax 1933). The chromosome number and morphology in the gymnosperms is best obtained from the haploid endosperm cells, but it was so difficult to obtain female cones from most cycads that root tip preparations have been used almost exclusively. The root tips were fixed in acetic acid alcohol, and aceto-carmine smears were made from this material.

Material for the cytological investigation has been obtained from a number of sources. Female cones of *Zamia* were obtained from Mr. Robert Gray, superintendent of the Atkins Institution of the Arnold Arboretum at Soledad, Cuba. Dr. Edgar Anderson obtained root tips from several genera at the New York Botanical Garden, and some material was sent from the University of Pennsylvania by Dr. Conway Zirkle. Most of the material was obtained from Dr. Chamberlain's collection of cycads at the University of Chicago by the junior author.

So far as possible, we have followed Schuster's classification of the Cycadaceae (Engler, 1932). The following genera and species have been studied:—*Cycas revoluta* Thunb., *C. circinalis* L., *C. Rumphii* Miq., *Bowenia serrulata* André, *Macrozamia tridentata* (Willd.) Regel, *M. Miquelii* (F. Muell.) Schuster, *M. Moorei* F. Muell., *Stangeria paradoxa* Th. Moore, *Encephalartos Altensteinii* Lehmann, *Dioon spinulosum* Dyer, *Microcycas calocoma* (Miq.) A. DC., *Ceratozamia*

mexicana Brongn., *C. mexicana* var. *longifolia* (Miq.) Schuster, *Zamia floridana* A. DC. and two varieties of *Z. media* Jacq., var. *Gutierrezii* (Sauvalle) Schuster and var. *portoricensis* (Urban) Schuster. Two species collected as *Cycas* "Wadel" and as *Zamia pumila* L., could not be placed definitely according to Schuster's classification.

The chromosomes can be studied most readily in the "endosperm" cells. A few such preparations were obtained from female cones of *Zamia*. The chromosomes of most species examined were studied in aceto-carmine smears of root tips. In most cases it was possible to determine the chromosome number and morphology quite accurately. The chromosomes are large and in the smear preparations they are spread out in nearly the same focal plane. Photographs of the somatic chromosomes of several genera are shown in plate 107. The chromosomes of other genera and species are pictured in plate 108. Only two good division figures were obtained from *Bowenia* and in these the chromosomes were so widely scattered in smearing that it was impracticable to represent them in the photographs or drawings. *Dioon* also proved to be difficult, and in *D. edule* there appeared to be only 16 chromosomes in some figures, but these were not clear enough to establish a definite count. The chromosome numbers of *Zamia* species were obtained from both endosperm and root tips. A summary of the chromosome number and morphology of the different genera is shown in table I.

TABLE I.

CHROMOSOMES OF CYCADS

Species	Terminal fiber	sub-term. fiber	median fiber	Total 2 n.
Cycas revoluta	10	8	4	22
Cycas circinalis	10	8	4	22
Cycas Rumphii	10	8	4	22
Bowenia serrulata		6	12	18
Macrozamia tridentata	2	6	10	18
Macrozamia Miquelii	2	6	10	18
Macrozamia Moorei	2	6	10	18
Stangeria paradoxa	2	2	12	16
Encephalartos Altensteinii		4	12	16
Dioon spinulosum		10	8	18
Microcycas calocoma	22	2	2	26
Ceratozamia mexicana		4	12	16
C. mexicana var. longifolia		4	12	16
Zamia media				
var. Gutierrezii		4	12	16
var. Commeliniana		4	12	16
var. portoricensis		4	12	16
Zamia floridana		4	12	16

In several genera, chromosomes are found with apparently terminal spindle fiber attachment points. These are especially clear as the chromosomes begin to separate at late metaphase. There is so much variation in chromosome size in different cells of a single individual that it was seldom possible to establish any consistent difference in chromosome size in different genera. The chromosomes of *Cycas* seem to be relatively shorter than those of other genera. The relative lengths of the chromosomes and the positions of the spindle fiber attachment points are consistent within each genus.

The chromosome number and morphology may differ considerably in different genera but the genoms of the species within each genus seem to be very similar, a condition also found in the Coniferales (Sax and Sax 1933). *Zamia* and *Ceratozamia* are similar in chromosome number and morphology. According to Chamberlain (1926) these genera have been crossed and the *Zamia* (male) parent was found to be dominant in F_1. Both the cytological and genetic data would indicate that these two genera are closely related.

The chromosome numbers in the cycads differ from those in the typical conifers. The basic haploid numbers are 8, 9, 11, and 13 for the cycads and the lower numbers 8 and 9, are most characteristic. In the conifers the basic number is 12 for the Taxaceae, although recent studies indicate that *Podocarpus* has 20 pairs of chromosomes. The basic number is 12 for most *Abieteae* and 11 for the *Cupresseae* and *Taxodieae*, with the exception of *Sciadopitys* which has 10 pairs of chromosomes. The basic chromosome numbers are 12 for the Ginkgoales and 7 for the Gnetales. The chromosomes are large in most gymnosperms, but *Gnetum* has a large number of relatively small chromosomes.

In general the chromosome numbers show some correlation with the taxonomic grouping of the gymnosperms. There is, however, little cytological evidence for any relation between existing gymnosperms and the angiosperms. If the angiosperms have been derived from the gymnosperms we must go back to extinct forms for the ancestral types.

SUMMARY

The haploid chromosome numbers in the Cycadaceae are as follows: *Cycas* 11, *Bowenia* 9, *Macrozamia* 9, *Stangeria* 8, *Encephalartos* 8, *Dioon* 9, *Microcycas* 13, *Ceratozamia* 8, and *Zamia* 8. Different genera may vary considerably in chromosome morphology, but species within each genus have similar chromosomes.

LITERATURE CITED

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EXPLANATION OF PLATES

PLATE 107

Photographs of cycad chromosomes. Aceto-carmine smears of root tips.
Photo. 1. Cycas revoluta.
Photo. 2. Microcycas calocoma.
Photo. 3. Zamia media var. portoricensis.
Photo. 4. Zamia pumila.

PLATE 108

Chromosomes of cycads.
Aceto-carmine smears. × 1000.
Figs. 1-7 from root tip cells. Fig. 8 from endosperms.

Fig. 1. Cycas revoluta.
Fig. 2. Cycas "Wadel."
Fig. 3. Macrozamia tridentata.
Fig. 4. Stangeria paradoxa.
Fig. 5. Encephalartos Altensteinii.
Fig. 6. Dioon spinulosum.
Fig. 7. Ceratozamia mexicana.
Fig. 8. Zamia media var. Gutierrezii.

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